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Will altered climate affect a discrete population of the sea urchin *Strongylocentrotus droebachiensis*?

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ABSTRACT

The Green sea urchin *Strongylocentrotus droebachiensis* is a cold-water species that in the 70s and 80s was the main culprit in the major grazing of macrophytes in the Norwegian fjords and coastal areas.

Recent reports have questioned a decline in the *S. droebachiensis* in the Oslofjord, similar to what was observed to occur in the Norwegian coastal population of *S. droebachiensis* after the 1990s. In surveys from 2013 we collected data on urchin density, test diameter, early urchin settlement and Gonad Index and created a framework in order to investigate if the current Inner Oslofjord populations of *S. droebachiensis* are different from surveys conducted in 1979 and 1992. This study found significant differences in density, diameter and settlement over time. Highest density in 1992 was at 10 and 15 m, while being at 20 m in 2013. Urchin diameter at the station with most urchins was on average 5 cm in 1992 compared to 3 cm in 2013. Settlement differed both between the number of settlers between 1992 and 2013, and season for highest settlement (summer in 1992, and autumn in 2013). The inner Oslofjord sea urchin data indicate a still healthy population, although environmental data (as temperature and salinity) have changed to less favorable conditions for this species.

1. Introduction

The Green sea urchin (*Strongylocentrotus droebachiensis*) is a prominent grazer of coastal areas, and plays a vital role in coastal production by grazing macroalgae and turning lush macrophyte beds into barren grounds (Norderhaug and Christie, 2009). *S. droebachiensis'* species distribution is restricted to the Northern Atlantic and Pacific Oceans as well as the Arctic Ocean. It's southern distribution limit is New Jersey USA in the Northwest Atlantic and Northern Denmark in Northeast (Hayward and Ryland, 1990; Mortensen, 1924). The sea urchin dominates a large coastal area along the coast of Northern Norway while further south only restricted to some fjords south to the Skagerrak area. Among these more discrete sea urchin populations the one in the Oslofjord, has been frequently monitored (Källqvist et al., 1982; Magnusson et al., 1984a, 1984b, 1992) and studied (Fredriksen, 1999; Frid and Thomassen, 1995; Green, 1983).

It has been hypothesised that *S. droebachiensis* have been grazing regularly since the last ice age in many of Norway's southern fjords, including the Oslofjord (Vasseur, 1952; Anon, 2002). *S. droebachiensis* is vulnerable to high water temperatures, which is likely to be the reason why the species experienced a northward retreat (Fig. 1) along the Norwegian coast in the 80s and 90s (Fagerli et al., 2013; Rinde et al., 2014). This has given the kelp a possibility to recover on the coast from the 1990s (Skadsheim et al., 1995). The sea urchins retreated up to 64.5°N in 2007 (Norderhaug and Christie, 2009) and in more recent times further regrowth of kelp has been reported almost as far north as 67°N (Rinde et al., 2014).

While the *S. droebachiensis* population has been retreating northward on the coast, there are no data on how urchin population in southern fjords, like the Oslofjord, are affected. This is the main point of interest in this study, as the Oslofjord is located further south (at 59°N) than current southernmost distribution (at 67°N) of coastal populations of the *S. droebachiensis*. Until recent the Oslofjord *S. droebachiensis* population seemed to appear unaffected by rising coastal water temperatures and it is possible that the isolating effect of the fjord's morphology and hydrography is what has allowed the populations there to persist so far south (Fredriksen, 1999; Norderhaug and Christie, 2009).

An important characteristic for the sea urchin populations in the Oslofjord is the hyposaline top layer water body created by the outflow of two large rivers in the outer part of the fjord (Walday et al., 2014). Since sea urchins are vulnerable to low salinities (Lange, 1964) this hyposaline water body may force the sea urchin to stay deeper and

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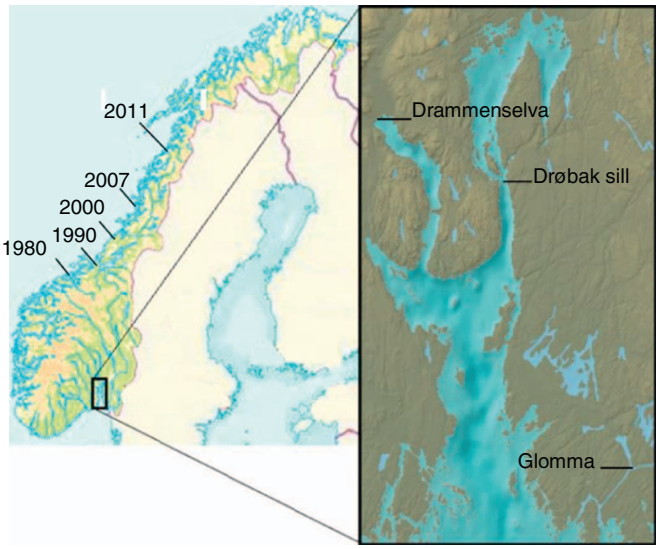

Fig. 1. Overview map of Norway and the enlarged image is of the Oslofjord. The black lines represent the southern border of the urchin barrens at different times. The Drøbak sill, Drammenselva and Glomma are pinpointed in the enlarged image.

prevent exchange of larvae with the outer coast. Also the Inner Oslofjord is isolated from the Outer Oslofjord by the Drøbak sill (Fig. 1), which at the shallowest is 20 m deep, thus separates the deep-water of the inner basins from the outer basins for long periods, especially during the stratification in the Spring (Staalstrøm et al., 2012). The combination of a shallow sill, seasonal stratification and water circulation around the Drøbak sill may create a low connectivity between the outer and inner fjord urchin populations. This low connectivity can be further strengthened by the surface water flowing out. However, as ocean water temperatures continue to rise as climate change progresses, the morphology of the Oslofjord will also restrict migration of the urchins into suitably cooler waters. High resolution analyses of sea surface temperatures have shown that coastal regions are heating up quicker than offshore regions (Lima and Wethey, 2012). As *S.droebachiensis* is a cold-water species, it will most likely be strongly affected by the temperature and precipitation (salinity) changes predicted by IPCC (2013).

Some observations by scientists conducting research in the area have drawn attention to the possibility that the urchin population may be declining in the southernmost and isolated fjords in Scandinavia as well, specifically Gullmars-, Oslo- and Lysefjord (observations by H. Christie, K.M. Norderhaug and E. Svensen).

The aim of this study was to investigate the current density, size-distribution, settlement and/or gonad production of the Oslofjord *S. droebachiensis* population and to compare this to available historical data. Gonad Index can be used as a proxy to estimate the condition of the population, mostly with regards to food quality and supply (Himmelman, 1984; Raymond and Scheibling, 1987; Vadas, 1977).

2. Methods

The study used three different urchin sampling stations in the inner Oslofjord where data from previous studies were available (Fig. 2). Urchin sampling station 1 (Station 1) was located at the Drøbak sill (59.66°N, 10.63°E), and was the study's outermost sampling station. Urchin sampling station 2 (Station 2) was on the western side of the Nesodden peninsula, in The Vestfjord (59.86°N, 10.65°E), while urchin sampling station 3 (Station 3) was the innermost sampling station in this study, located in the Bunnefjord (59.78°N, 10.73°E). There were three sampling sessions per station, one in Spring, one in Summer and one during Autumn. The Spring sampling at Station 1 and Station 2

Fig. 2. Overview map of the Inner Oslofjord. Stations used in this study are pinpointed.

took place on 26 March 2013, while the collection at Station 3 was conducted on 23 May 2013 due to ice cover in March. The Summer sampling was on 28 June 2013 at all stations, and the Autumn sampling was done on 3 October 2013. The availability of data from prior studies on *S.droebachiensis* populations varied between stations. This study compares current data to three previous studies; one study from 1979 at Station 2 on density and size distribution (Green, 1983), and two studies from 1992 at Station 1, one about urchin settlement (Frid and Thomassen, 1995) and one about density, size distribution and Gonad Index (Fredriksen, 1999). Station 3 had no data from prior studies to compare with.

2.1. Density and size measurements

The density counts and collection of urchin specimens were conducted by SCUBA diver. Four depths were assessed in this study: 5, 10, 15 and 20 m. For density counts, the diver swam at the depth in question and dropped a 0.25 m^2 square frame at random ten times. This is similar to what prior studies have done. The number of sea urchins within the square frame was registered by the SCUBA diver and reported to the crew on land using a communication cable. As far as possible, 100 urchins per depth were also collected at each sampling station, which were later used in analysis of the demographics between depths and stations. The individuals were collected in the same plots used for the density counts to get a representative sample from the locations. All sea urchins inside each frame including the last frame were collected. If the density at a certain depth was low, the diver would collect all individuals found at that depth within the available time (15 mins per depth). The individuals were placed into nets labelled with the station and depth and kept separate.

The collected urchins were analysed in the laboratory within two weeks after collection. The size of the individuals was measured immediately or stored in a freezer for later processing. The diameter of the sea urchins was measured to the nearest millimetre using a calliper. Size was used as a proxy for the age of the individual, as the 1 cm/year

growth rate is an indicator of urchin age (Robinson and MacIntyre, 1997; Vadas et al., 2002) until the individual reaches approximately four to 5 cm (Fagerli et al., 2015; Russell and Meredith, 2000), unless food sources are scarce (Larson et al., 1980).

2.2. Settlement

Standardized collection units were placed at four depths (5; 10; 15 and 20 m) at each station in order to assess the recruitment success in the fjord. These units consisted of four pan scours, which is a 15-cm woollen ball made out of thin threads of steel. The brand used is named 'Vileda'. The scours were attached to a two metres long chain and are suitable for comparative sampling of urchin settlement (see *e.g.* Fagerli et al., 2013). Four scours were attached to the chain with cable ties, approximately 0.5 m apart. The scours were collected and sealed individually *in situ* and the units were replaced during the next sampling session. There was one chain with scours attached at each depth and at each station.

On shore, the scour sample with early urchin settlers was fixed in 70% alcohol and stored in a dark and well-ventilated area. Over the duration of this study 15 of the 24 chains were lost, and it is believed that this was caused by fishing activity on location. Four were lost from Station 1, five from Station 2 and six from Station 3.

In the lab, the scours were cut into pieces and rinsed in freshwater and emptied into a 250 μm sieve to retrieve all organisms. Early settlers have a size of 500 μm and up, so the mesh size was small enough to avoid loss of settlers. The content was then transferred to a petri dish and counted using a dissecting scope under 2 × magnification.

2.3. Gonad production

Individuals collected during the second and third sampling sessions (Summer and Autumn, respectively), and larger than 3.5 cm in diameter, were wet weighed using an electronic scale and then the gonads were extracted in order to weigh this separately. These were done to calculate Gonad Index for the individuals, in accordance with James and Siikavuopio's (2012) guide to reproductive assessment.

The formula to determine Gonad Index is:

$$\mathrm{GI}\ (\%) = \frac{\text{Wet weight (g) of gonads}}{\text{Total wet weight (g) of sea urchin}} \times 100$$

2.4. Environmental data

Temperature and salinity data from the Inner Oslofjord were used in order to see if there has been recorded any changes in annual mean temperature or salinity since then. This data was provided by the *Academic Council of Water and Sewage Technical Cooperation in the Inner Oslofjord*, and came from environmental monitoring stations less than five kilometres away from the urchin sampling stations. Temperature and salinity measurements from the most adjacent depths were used, in order to correlate with the registered sea urchins. Environmental measurements were taken throughout the year, and this study used records spanning from 1999 up until 2009 at Station 1, 1973 to 2010 at Station 2, and from 1945 to 2012 at Station 3. There were gaps in the data, both temporally and spatially. Temporally, the data gap from Station 2 spanned from 1977 to 1993, at Station 3 it spanned from 1962 to 1973. These gaps are caused by a lack of environmental monitoring in these timespans. Spatially, Station 1 had measurements from five metres depth, while Station 2 and Station 3 measured salinity and temperature at four metres. These depths were used as these had the longest and most consistent datasets.

2.5. Data analysis

Crossed ANOVAs performed in the R x64 3.4.1 package was used to statistically analyse the data. This study used a crossed design to analyse all the interactions between factors. The sampling session factor had three levels; Spring, Summer and Autumn. Station factor had three levels; Station 1, Station 2 and Station 3, while depth had four; 5, 10, 15 and 20 m. We tested for significant differences between sampling year (when including historical data), season, station and depth, and for interactions between the respective variables.

The statistical analyses were divided into two parts; first part analysed data from previous years with 2013 at the Stations which had prior data, and the second part looked at all data from 2013 to analyse differences between the stations. Station and depth were used as fixed factors. Station was used as a fixed factor because the sampling conducted in this study, and the prior ones, were done at the same locations. The ANOVA tests on urchin diameter and urchin density analysed three factors and their interactions: season, depth and either year or season, depending if the test was to investigate differences between urchin sampling in years or at stations. This applied for the ANOVAs on GI and settlement as well. However, the season factor for early urchin settlement had only two levels (Summer and Autumn). To compare changes in environmental factors we performed a linear regression on the datasets from four or five metres, as these are the shallowest depths we investigated, had long datasets and fewest gaps in measurements, which could skew any analyses.

3. Results

3.1. Size distribution

The study found that larger urchins were found deeper in the water column, while smaller individuals were at shallower depths. At the spring sampling (Fig. 3, a–c) no urchins were found at five metres at any stations. Most individuals were at 20 and 15 m and were larger than two centimetres.

In general, most of the individuals were in the 2.1–2.5 and 2.6–3.0 cm size classes. It was found an even distribution of large individuals (diameter larger than four cm) at 20 m depth at station 1 (Fig. 3, a). Station 2 (Fig. 3, b) presented a bimodal curve for the individuals found at 15 and 20 m, both with their peaks at 1.1–1.5 cm and 2.6–3.0 cm size classes. Station 3 had the fewest individuals registered (130 individuals) in the whole study (Fig. 3, c).

The summer sampling (Fig. 3, d–f) presented a size-segregation by depth where the larger individuals were found deeper than the smaller ones. As in spring, no sea urchins were registered at five metres. The distribution at Station 1 at 10 m had a peak at the 1.1–1.5 cm size class. At 20 m the size frequency peaked around 3.1–3.5 cm. No sea urchins were found at 15 m. Station 2 exhibited a bimodal curve at 20 m, with a big peak at 1.1–1.5 cm and a smaller one at 2.6–3.0 cm (Fig. 3, e). At 15 m there was one peak at 2.1–2.5 cm. Station 3 (Fig. 3, f) had one dominant size class at 20 m, 2.1–2.5 cm, with 61 of the 153 individuals in this category. At 15 m, station 3 presented a bimodal distribution with peaks at 1.6–2.0 cm and 3.1–3.5 cm.

The autumn sampling (Fig. 3, g–i) was the only time where sea urchins were found at all depths. Almost all individuals were located at 20 m depth (263 individuals out of 294) at Station 1 (Fig. 3, g). The most abundant size class was 3.1–3.5 cm. Station 2 (Fig. 3, h) had the most individuals registered with a total of 719 individuals distributed between all depths and almost all size classes. At 15 and 20 m depths, it was found bimodal distributions with peaks in the 1.1–1.5 cm and 3.1–3.5 cm size classes. Only 194 individuals were registered at Station 3 (Fig. 3, i). The peak at five metres was in the 1.6–2.0 cm size class, while at 15 and 20 m the distribution peaked at 2.6–3.0 cm and 2.1–2.5 cm, respectively.

The average diameter of *S. droebachiensis* seemed uniform in 2013

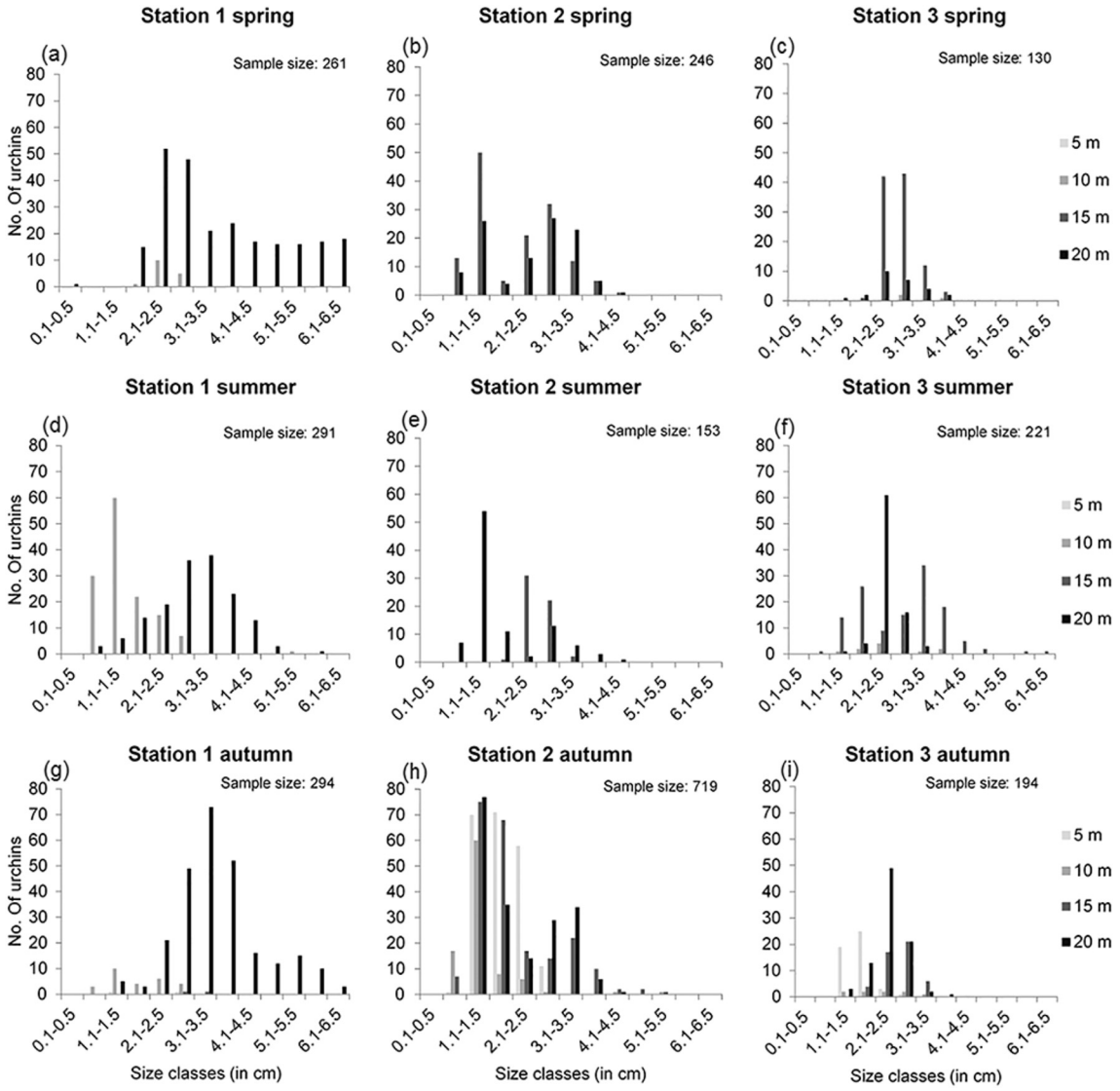

Fig. 3. Sea urchin *S. droebachiensis* size-distribution at Station 1 (a,d,g), Station 2 (b,e,h) and Station 3 (c,f,i) for the different seasons sampled. The x-axis represents 0.5 cm size classes from 0.1 to 6.5 cm. Y-axis is the number of urchin individuals in each size class.

(Fig. 4). The largest sea urchins were mainly found at deeper depths (20 m) than in shallower waters, except at Station 3. The data from Station 1 in 1992 registered much of large sea urchins at 10 and 15 m, while at Station 2 in 1979 had an average diameter larger than 3 cm at all depths.

Station 1's ANOVA (Table 1) found significant difference in all factors and interactions investigated. This shows that there is a difference in urchin diameter and at which depth the urchins stood at Station 1 between 1992 and 2013.

Year was the only significant factor (P = 0.03423) when analysing the urchin diameter between 1979 and 2013 at Station 2, showing that urchins at this sampling station were on average larger in 1979 than 2013 (Table 2).

The ANOVA test for urchin diameter in 2013 (Table 3) found significant differences between all factors and interactions. This shows that there is a difference in which depths the largers and smaller individuals are located, with larger individuals usually being found deeper than the smaller ones.

3.2. Urchin abundance

Urchin abundance and depth distribution varied between seasons at all stations. At Station 1 in 2013 (Fig. 5, b), the majority of individuals were found to occur at 20 m during all sampling seasons. However, the range of their depth distribution did vary throughout the year. In spring and summer urchins were only registered at 20 m, while in autumn, the urchins occurred at all four depths surveyed. The depth distribution at Station 1 in 1992 (see Fig. 5, a) showed that the majority of urchins occurred at 15 m. There were also more individuals occurring at five and 10 m depths than in 2013.

At Station 2 (Fig. 5, c) as well, the highest density was found at 20 m, except in spring where it was higher at 15 m (34.4 urchins/m^2). In summer, urchins were found at 10, 15 and 20 m, but the densities were lower than 10 urchins/m^2. The distribution gradually increased with depth during autumn, starting at 4.4 urchins/m^2 at five metres and ending up at 21.6 urchins/m^2 at 20 m.

Station 3 (Fig. 5, d) had a low density, < 10 urchins/m^2, at all depths and all seasons. Urchin abundance in autumn was the lowest at Station 3 of the different locations.

The variation in density between 1992 and 2013 at Station 1 (Table 4) was not found to be significant (P = 0.1269632). However, interaction between year and depth was highly significant (P = 0.0006223), which means that the urchin density at certain depths differed between the years. Depth as an individual factor was

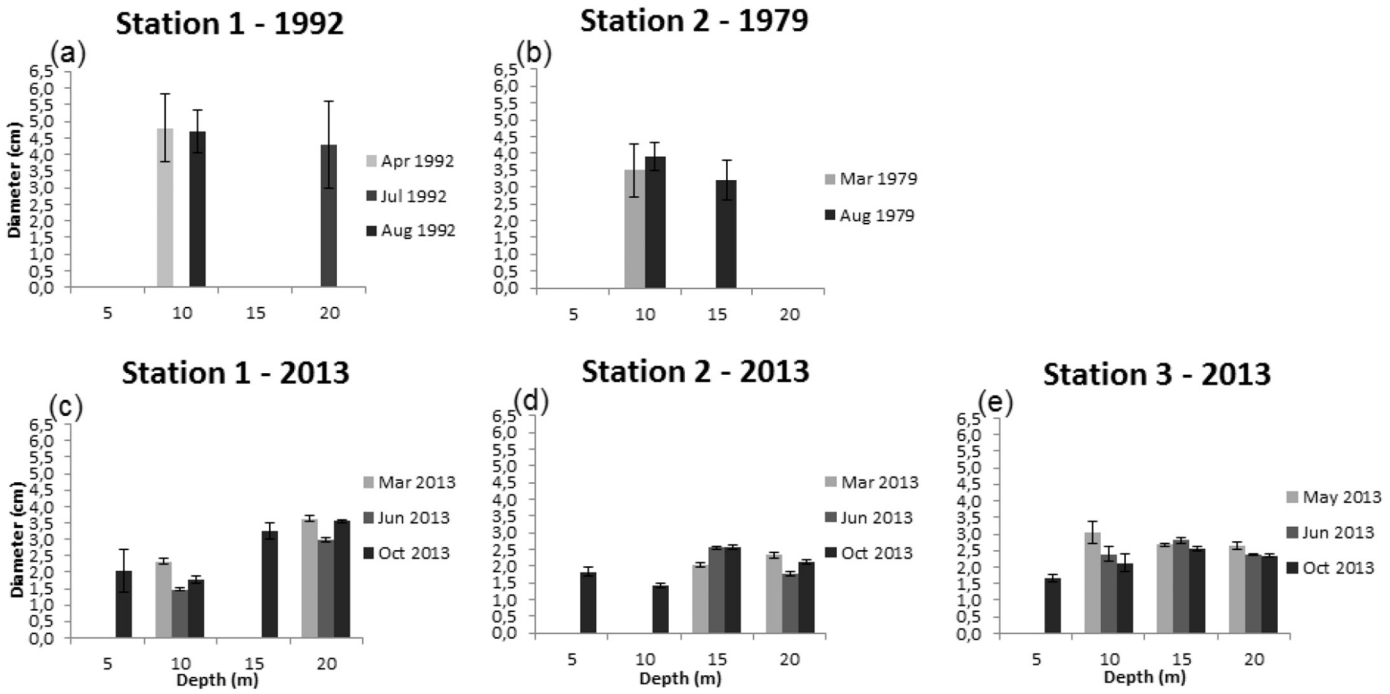

Fig. 4. Sea urchin *S. droebachiensis* average urchin diameter. Station 1 in 1992 (a) and 2013 (c), Station 2 in 1979 (b) and 2013 (d) and Station 3 in 2013 (e). Light grey colours signify spring season, medium-grey summer and dark grey autumn. The y-axis is the different depths where the diver stopped and collected sea urchins for measurements. X-axis shows the average diameter at the different depths. Error bars represent Standard Error.

Table 1
ANOVA test on the average urchin diameter at Station 1. The factors are year, depth and season on the average diameter of the sea urchins, and the interactions between year and depth, and year and season. Response variable was average urchin diameter. P-values < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)	
Year	1	17.2288	17.2288	173.1124	$3.42 * 10^{-6}$	***
Depth	4	1.6896	0.4224	4.2442	0.046764	*
Season	2	1.3383	0.6691	401.483	0.0002271	***
Year:depth	1	1.6371	1.6371	16.4488	0.004836	**
Year:season	1	0.1347	0.1347	29.397	0.0056099	**
Residuals	4	0.0183	0.0046			

Table 2
ANOVA test on the average urchin diameter at Station 2. The factors are year, depth and season on the average diameter of the sea urchins, and the interactions between year and depth, and year and season. Response variable was average urchin diameter. P-values < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)	
Year	1	4.4824	4.4824	27.7263	0.03423	*
Depth	3	0.2502	0.0834	0.5159	0.71187	
Season	2	0.0323	0.0162	0.0999	0.90917	
Year:depth	1	0.8333	0.8333	5.1546	0.15120	
Year:season	1	0.0675	0.0675	0.4175	0.58442	
Residuals	2	0.3233	0.1617			

also significant (P = 0.0071263) and the year-season interaction was also found to be significant (0.0078750).

Depth was found to be highly significant (P = 0.0003931) for the urchin density in 2013 (Table 5), meaning that there is a pattern of higher densities of urchins at lower depths. Station was also found to be significant (P = 0.0409640), with fewer individuals at Station 3 than Station 2 and Station 1, respectively. Season was not found to be significant, but the interaction between station and season was (P = 0.0112230).

Table 3
ANOVA test on the average urchin diameter in 2013. The factors are station, depth and season on the average diameter of the sea urchins, and the interactions between station and depth, and station and season. Response variable was average urchin diameter. P-values < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)	
Station	2	1.2655	0.63277	37.7147	0.002536	**
Depth	3	3.6211	1.20704	71.9426	0.000617	***
Season	2	0.3988	0.19939	11.8844	0.020749	*
Station:depth	6	2.3078	0.38463	22.9249	0.004613	**
Station:season	4	0.4489	0.11222	6.6887	0.046347	*
Season:depth	4	0.5173	0.12933	7.7086	0.036529	*
Residuals	4	0.0671	0.01678			

3.3. Urchin settlement

The majority of settlement at Station 1 in 2013 occurred at 10 m both during summer and autumn (Fig. 6, b). There were no early settlers registered at any other depth during the summer sampling, and only very few individuals at 15 and 20 metres during autumn. The size of the early settlers ranged from 500 μm to 2 mm. Some of the chains with scours were lost.

The scours in 1992 (Fig. 6, a) had a high number of settlers (over 15 settlers/scour) at all depths during autumn. At the most it was an average of 26.8 settlers/scour (15 m). The highest average number during summer settlement occurred at 10 m, and was 1.3 settlers/scour. Urchins were found at other depths, though these were less than one per scour. The scours that were collected at Station 2 (Fig. 6, c) had a higher number of recruits at 10 m, with an average of 50 settlers per scour during Summer. Station 1 and Station 2 seemed to have approximately the same number of settlers in the autumn, though at Station 2 they were found only at 10 m.

Settlement at Station 3 (Fig. 6, d) yielded an average of 20.3 settlers per scours at 15 m during summer (no scours were found at any other depth during this season). In the autumn sampling, some settlers were found at five metres (but again, no scours were found at any depth

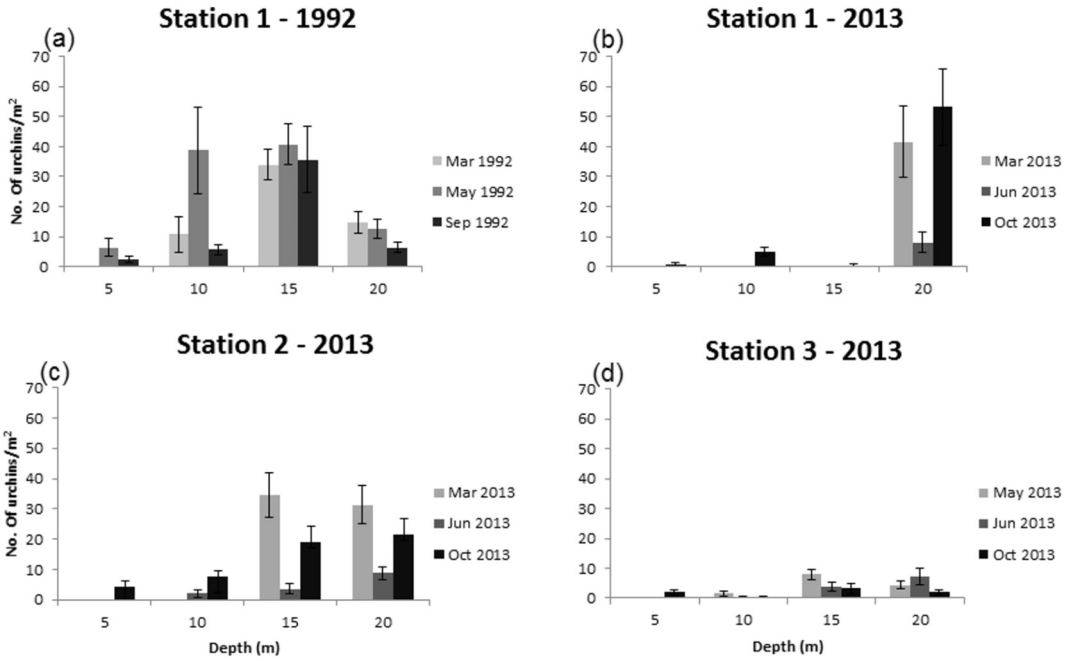

Fig. 5. Sea urchin *S. droebachiensis* average density distribution with depth. Data from Station 1 in 1992 (a), Station 1 in 2013 (b), Station 2 2013 (c) and Station 3 2013 (d). The y-axis is the different depths where sea urchins were registered. X-axis shows the average number of sea urchins per square metre (urchin/m^2) at the different depths. Error bars represent Standard Error.

Table 4
ANOVA test on the average urchin density at Station 1. The factors are year, depth and season on the number of sea urchins registered, and the interactions between year and season, year and depth, and depth and season. Response variable was average urchin density. P-values < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)	
Year	1	177.19	177.19	2.7709	0.1269632	
Season	2	108.58	54.29	0.8490	0.4564899	
Depth	3	1395.30	465.10	7.2733	0.0071263	**
Year:season	2	1045.40	522.70	8.1741	0.0078750	**
Year:depth	3	2717.90	905.97	14.1677	0.0006223	***
Season:depth	6	883.49	147.25	2.3027	0.1157670	
Residuals	10	639.46	63.95			

Table 5
ANOVA test on the average urchin density in 2013. The factors are station, depth and season on the number of sea urchins registered, and the interactions between station and season, station and depth, and depth and season. Response variable was average urchin density. P-values < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)	
Station	2	450.32	225.16	4.1265	0.0409640	*
Season	2	389.60	194.80	3.5701	0.0581060	.
Depth	3	2048.80	682.93	12.5160	0.0003931	***
Station:season	3	308.24	102.75	1.8830	0.0112230	*
Station:depth	6	1468.36	244.73	4.4851	0.1823027	
Season:depth	6	512.18	85.36	1.5645	0.2340845	
Residuals	13	709.34	54.56			

besides this).

ANOVA testing for any significant effect by year, season, depth or the interaction between year and season (Table 6) at urchin settlement at Station 1 showed that year, season and the interaction between year and season were significant. This indicates that there was a significant difference in settlement between 1992 and 2013. Most of the settlement occurred during autumn in 1992 and Summer in 2013, and there were more early settlers in 1992 than 2013. This may indicate a difference in seasonal patterns among study years.

Regarding settlement in 2013, the ANOVA (Table 7) did not find any significant effect on the urchin settlement by either station, season, depth or the interaction between station and depth.

3.4. Gonad index

GI in sea urchins sampled at Station 1, Station 2 and Station 3 in 2013 (Fig. 7, b,c d) exhibited the same variation of GI, between 5% and 15%, as the sampling done in 1992 (Fig. 7, a). This study found that GI was highest at summer in 2013. The urchins from Station 1 possessed the highest GI during both Summer and Autumn.

The ANOVA test on GI at Station 1 did not find any significant effect of year, season, depth or the interaction between year and depth (Table 8). Year and depth were almost deemed significant (P = 0.05567 and P = 0.06292).

Similar to the ANOVA on Station 1, when analysing the effect of station, season, depth and the interaction between station and depth on the GI collected in 2013 (Table 9), no significant effect was found.

3.5. Environmental data

Temperature data from all stations showed an increase in mean temperature at four or five metres (Fig. 8). The mean temperature increase at Station 1 was 1.0 °C from 1999 to 2009, while at Station 2 increase was 0.9 °C from 1973 to 2010, and finally at Station 3 the change in mean temperature was 3.0 °C from 1945 to 2007.

Regarding salinity (Fig. 9), the data showed a decrease in mean salinity at four or five metres depth at all stations. Station 1 showed a drop from 1999 to 2009 by one ppt (parts per thousand), the same drop as was discovered at Station 2 from 1973 to 2010. Station 3 showed a decrease by almost two ppt from 1945 to 2007.

4. Discussion

The *S. droebachiensis* population in the Inner Oslofjord appears to remain in a healthy state as opposed to the collapsing coastal populations in Mid Norway (Fagerli et al., 2013; Rinde et al., 2014). There are indications of significant changes in the Oslofjord urchin population, as

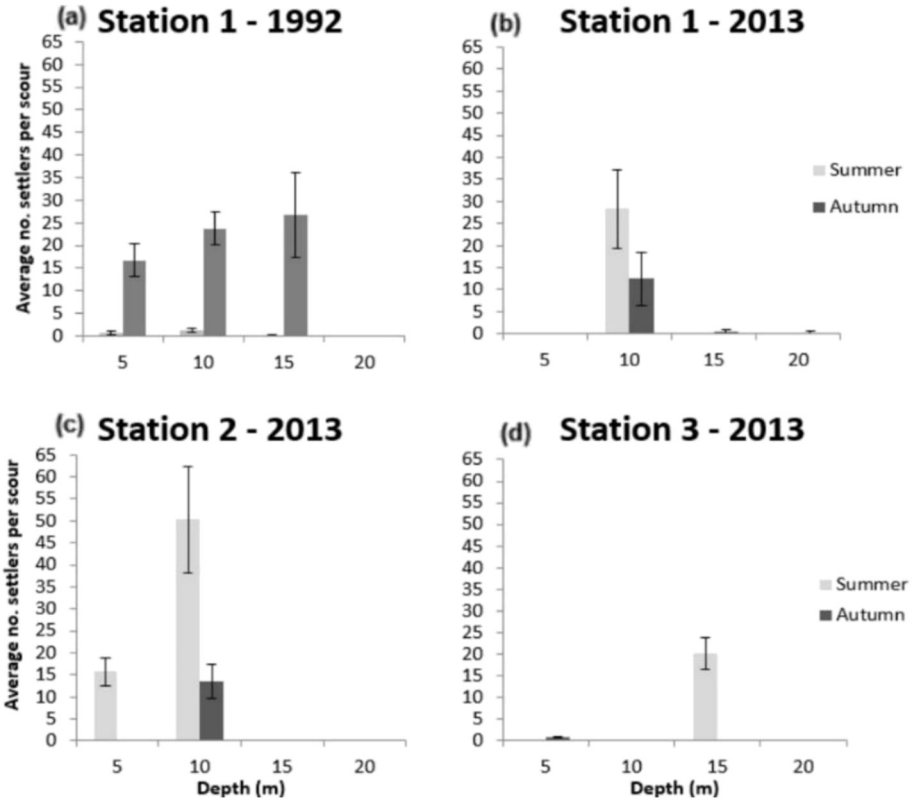

Fig. 6. Sea urchin *S. droebachiensis* average number of settlers per scour. Station 1 in 1992 (a), Station 1 in 2013 (b), Station 2 in 2013 (c) and Station 3 in 2013 (d). The x-axis represents the different depths where the scours were collected from. Y-axis is average number of settlers per scour. The scours in the 1992 summer sampling were collected between March and July, and the 1992 autumn sampling was collected between July and December. Error bars represent Standard Error.

Table 6
ANOVA test on the average number of settlers per day at Station 1. The factors are year, season and depth. The interaction between year and season was analysed. Response variable was average number of settlers per day. P values < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)	
Year	1	300.83	300.83	31.3004	0.011280	*
Season	1	447.68	447.68	46.5789	0.006436	**
Depth	3	58.07	19.36	2.0139	0.289941	
Year:season	1	223.70	223.70	23.2753	0.016972	*
Residuals	3	28.83	9.61			

Table 7
ANOVA test on the average number of settlers per day in 2013. The factors are station, season and depth. The interaction between station and depth was analysed. Response variable was average number of settlers per day. P values < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)
Station	2	1.0660	0.5330	2.6321	0.3995
Season	1	3.0956	3.0956	15.2870	0.1594
Depth	3	1.6662	0.5554	2.7427	0.4114
Station:depth	1	0.0016	0.0016	0.0079	0.9436
Residuals	1	0.2025	0.2025		

shown by the differences in abundance, size-distribution and recruitment in 2013 compared to the previous studies (Fredriksen, 1999; Frid and Thomassen, 1995; Green, 1983). Then, some small but significant differences within these parameters may indicate a more uncertain future for this *S. droebachiensis* population in the inner Oslofjord. There were particularly three differences: (1) the seasonal and depth abundance distributions showed the majority of individuals being registered at greater depths and in the later seasons of 2013 than compared to 1992 (see Fig. 5). This may indicate a preference of greater depths to avoid increasing temperatures and decreasing salinity in the upper water masses (see Table 4 and Figs. 5, 8 and 9). (2) the average test diameter of *S. droebachiensis* was smaller (see Table 1, Table 2 and Fig. 4) and (3) urchin settlement was lower in 2013 compared to 1992 (Fig. 6, Table 6). Although these differences were observed, it is quite difficult to draw any substantial conclusions about trends in the urchin demographic and density over the past 34 years, as this study could only compare data from three years (1979, 1992 and 2013), though these years were quite similar in high and low temperatures (Fig. 8).

This study found sea urchins in all size classes at all stations, with mostly the two or three centimetres size classes dominating (Fig. 3). If size is a proxy for age, this finding shows that there most likely were two strong recruitment years in 2010 and 2011, which had water temperatures higher than the suggested lethal threshold of 10 °C. In addition, due to the broad size range found in this study, it is believed that settlement is regular in the Inner Oslofjord (Fig. 6, Table 7). On the other hand, Station 3 showed a narrow range in size distribution (Fig. 3 (c,f,i)), indicating that the urchins at Station 3 might be more dependent on strong recruitment years, similar to what Sivertsen (2006) claims generally to be case for urchin populations. However, the regularity found at the other stations points towards annual recruitment, more aligned with what Leinaas and Christie (1996) suggest to be normal. The difference found at Station 3 could be caused by the morphology of the fjord, as Station 3 is the innermost station and hence the most isolated station used in this study (Fig. 2).

The average diameter of *S. droebachiensis* in the Oslofjord has decreased in comparison to data from previous studies (Fig. 4; Tables 1, 2). The mean size found in the current survey was almost 2.5 cm smaller at Station 1 than in 1992 (Fredriksen, 1999), and 1.0 cm smaller at Station 2 compared to in 1979 (Green, 1983). The majority of large individuals were found at 15 and 20 m (Fig. 3). The high abundance of small urchins (Fig. 3) at shallower depths, suggests that larger, anticipated older individuals may be standing deeper than 20 m and thus outside of this study's survey area. This explanation appears particularly appropriate for Station 1, as 80 of the 84 specimens larger than 5.0 cm were found there. In fact, the urchins at Station 1 were generally

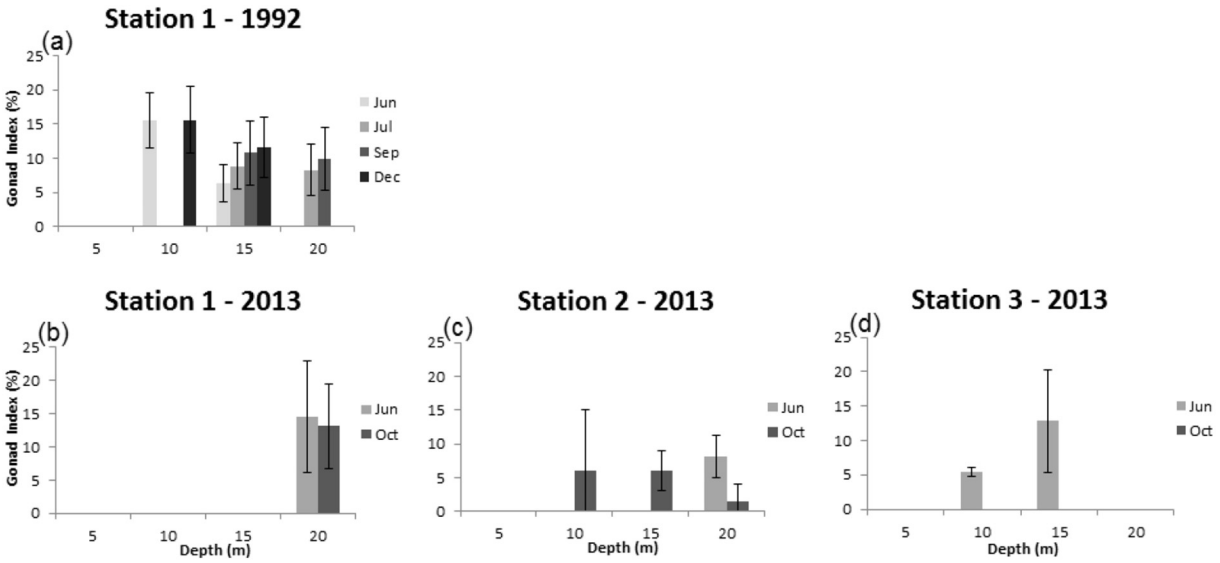

Fig. 7. Sea urchin *S. droebachiensis* average Gonad index. Station 1 in 1992 (a), Station 1 in 2013 (b), Station 2 in 2013 (c) and Station 3 in 2013 (d). The x-axis represents the depth where the sea urchins were collected from, and the y-axis is the gonad index (% of total urchin weight that is gonads). Summer sampling occurred June 28th, and autumn sampling was October 3rd. Error bars represent Standard Error.

Table 8
ANOVA test on Gonad Index (GI) at Station 1. The factors are year, season and depth. The interaction between year and depth was examined. Response variable was GI. P value < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)	
Year	1	22.3942	22.3942	7.1416	0.05567	.
Season	2	20.163	10.0814	3.2150	0.14708	
Depth	2	37.461	18.7304	5.9732	0.06292	.
Year:depth	1	7.7960	7.7960	2.4862	0.18998	
Residuals	4	12.543	3.1358			

Table 9
ANOVA test on Gonad Index (GI) in 2013. The factors are station, season and depth. The interaction between station and depth was examined. Response variable was GI. P value < 0.05 was deemed significant.

	Df	Sum sq	Mean sq	F value	Pr (> F)
Station	2	128.745	64.373	9.5226	0.2234
Season	1	10.379	10.379	1.5353	0.4323
Depth	2	15.326	7.663	1.1336	0.5532
Station:depth	3	20.651	6.884	1.0183	0.6053
Residuals	1	6.760	6.760		

larger than those from the other two stations (Table 3). The reason behind this pattern is uncertain, but in line with what was found in the transition zone between kelp bed and urchin barren (Gagnon et al., 2004), and at urchin barrens (Himmelman, 1986), is suggesting better food conditions for the urchins at Station 1.

The survey conducted for this study found less urchins at shallower depths (five and ten metres) compared to previous studies from the same locations (Fredriksen, 1999; Green, 1983). Fredriksen (1999) found *S.droebachiensis* at five and ten metres in all seasons in 1992, around ten urchins per square metre (Fig. 5), whereas the current study only found a few, if any at all. Compared to Fredriksen (1999), there were significant differences in depth distribution between 1992 and 2013 (Table 4), but not between stations in 2013 (Table 5). The majority of sea urchins were at 20 m in 2013, rather than at 10 and 15 m in 1992. This suggests that there might be a non-lethal factor, like temperature or salinity, pushing the population in to deeper water. Temperatures have increased at all stations (Fig. 7), while salinities have decreased (Fig. 8). Both are trends that are unfavourable as *S. droebachiensis* is vulnerable to high temperatures and low salinities (Foreman, 1977; Lange, 1964; Siikavuopio et al., 2008, 2012; Stephens, 1972). Neither our study or Fredriksen (1999) performed registrations of sea urchins below 20 m, but as earlier assessments of the species composition in the Oslofjord has found *S. droebachiensis* deeper than 20 m (Källqvist et al., 1982; Magnusson et al., 1984a, 1984b), they do most likely occur deeper than this study surveyed.

The seasonal distribution has also changed to fewer individuals in the spring and summer seasons 2013 compared to Fredriksen (1999) (Fig. 5). On the other hand, the seasonal pattern fits quite well with Ojeda and Dearborn's (1989) findings in Maine. Macroalgae is the most important food source for *S. droebachiensis* (Himmelman and Steele, 1971; Scheibling and Anthony, 2001), but the macroalgae in the inner Oslofjord inhabit only the upper ten metres (Berge et al., 2012, 2013), which seem to be seasonally out of reach for the sea urchins. However, *S. droebachiensis* is known to be omnivorous (Russell, 1998; Scheibling and Hatcher, 2001) and hence not entirely dependent on macroalgae to survive. There was a difference in urchin density between stations and season (Table 5). That pattern might be a result of differences in food availability between stations. There is no commercial or large-scale harvesting of *S. droebachiensis* in the Inner Oslofjord which could explain the change in seasonal distribution, or urchin density.

The early urchin settlement found in this study (Fig. 6) supports the claim of a stable abundance of *S. droebachiensis* in the Inner Oslofjord. However, settlement was found to occur in the summer in other *S. droebachiensis* populations studied (Fagerli et al., 2013; Falk-Petersen and Lønning, 1983; Miller and Emlet, 1997; Strathmann, 1978; Underwood and Fairweather, 1989). Compared to 1992 the present study showed a significantly lower rate of settlement (Fig. 6 and Table 6). This, combined with a stable gonad production, might indicate a lower survival of urchin settlersin the fjord. The temperature increase (Fig. 8) and salinity decrease (Fig. 9) might be the causes for this.

The study did not find any significant difference in GI comparing 2013 to 1992 (Table 8), or between stations (Table 9). In addition, GI was found to be at the same level as Meidel and Scheibling (1998) found in kelp beds and grazing fronts in Nova Scotia. This suggests that *S. droebachiensis* do have a stable supply of good quality food sources, which means the 1 cm/year growth rate found in *S. droebachiensis* (Fagerli et al., 2015) should be applicable for the Inner Oslofjord population. On the other hand, there are gaps in the GI data due to the

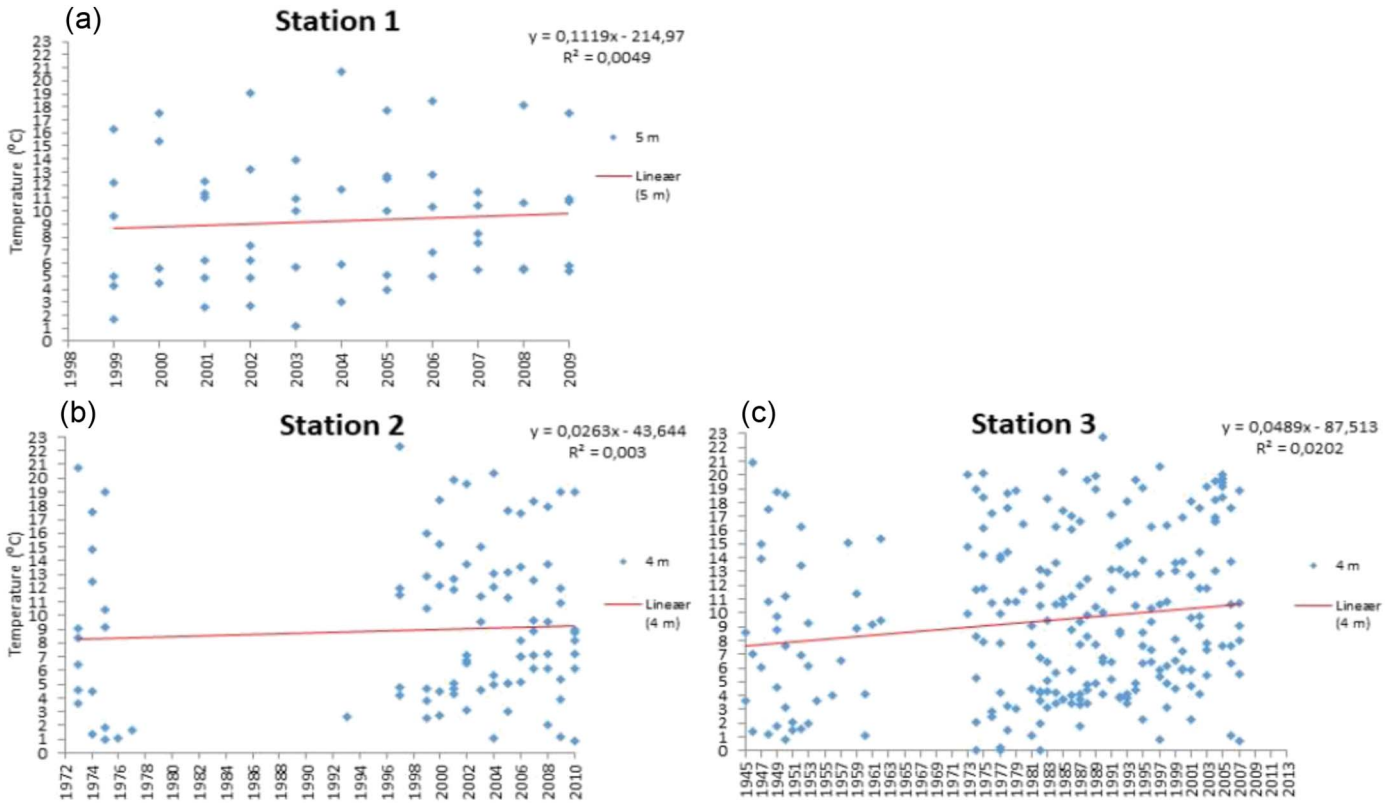

Fig. 8. Temporal changes in average water temperature at four or five metres depth in the Oslofjord. Station 1 (a), Station 2 (b) and Station 3 (c). The x-axis is the years where temperature was measured. Y-axis is the temperature, measured in Celsius, in the different years of the study period. The red line is the overall trend in the surveillance period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

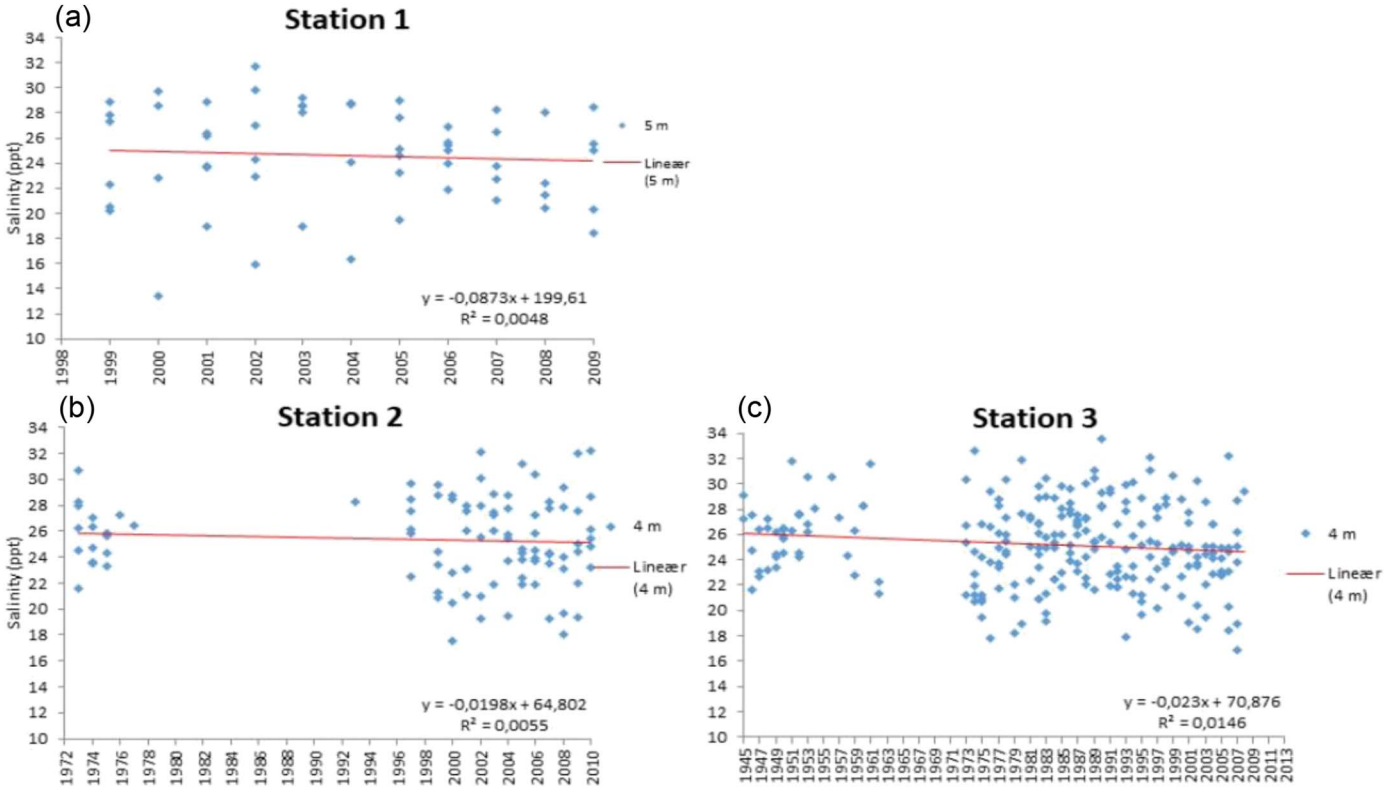

Fig. 9. Temporal changes in average salinity at four or five metres depth in the Oslofjord. Station 1 (a), Station 2 (b) and Station 3 (c). The x-axis is the years where salinity was measured. Y-axis is the salinity, measured in parts per thousand (ppt), in the different years of the study period. The red line is the overall trend in the surveillance period. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lack of large adults. In addition, the standard deviations for GI were also quite high and varying greatly between depth. There were many urchin individuals with little or no gonads, which might indicate some sort of stress factor affecting the urchin population and may be a concern for future recruitment. However, a few individuals with a large amount of reproductive material, as the large ones at Station 1, may compensate for the lack of gonads in others. Ebert (1985) found that fitness increased exponentially with test diameter.

Figs. 8 and 9 show long-term changes in temperatures and salinities that disfavour the *S. droebachiensis* population in the fjord, with strong seasonal fluctuations and with colder and more saline conditions with depths. An upper limit for larval and juvenile development found at 10 °C (Foreman, 1977; Stephens, 1972), and slightly higher temperature tolerance have been found for the adults (Hart and Scheibling, 1988; McEdwards, 1985; Pearce et al., 2005; Siikavuopio et al., 2008, 2012; Strathmann, 1978). This sensitivity to summer season temperatures will probably together with the sensibility to low salinities force the urchins to vertical migrations with seasons, but always below the top layer.

Our study concludes that the inner Oslofjord population is able to sustain, but with a vertical distribution deeper than the populations along the coast further north (see Norderhaug and Christie, 2009). The size-distribution and urchin settlement data suggests regularly turnover in the population rather than sporadically renewal by a few strong year classes. If the local recruitment is not regular, the population can be sustained by receiving settlers from other populations. There are no known coastal populations just outside of the inner Oslofjord, but there are urchin populations along the Danish coast that theoretically could replenish the Oslofjord population (Norderhaug et al., 2016). However, because of the isolating effect a fjord can exhibit due to the morphology of the fjord, with a shallow water sill and a major freshwater outlet at the opening (Walday et al., 2014), the supply of larvae from outside may be limited. A possible explanation for the maintaining isolated population may be that the water masses below the surface layer act as retention area for the sea urchin larvae as also suggested by Fredriksen (1999).

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